Title:

Ecological mechanisms explaining interactions within plant-hummingbird networks: Morphological matching increases towards lower latitudes

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Abstract

Interactions between species are influenced by different ecological mechanisms, such as morphological matching, phenological overlap, and species abundances. How these mechanisms explain interaction frequencies across environmental gradients remains poorly understood. Consequently, we also know little about the mechanisms that drive the geographical patterns in network structure, such as complementary specialization and modularity. Here, we use data on morphologies, phenologies and abundances to explain interaction frequencies between hummingbirds and plants at a large geographic scale. For 24 quantitative networks sampled throughout the Americas, we found that the tendency of species to interact with morphologically matching partners contributed to specialized and modular network structures. Morphological matching best explained interaction frequencies in networks found closer to the equator and in areas with low temperature seasonality. When comparing the three ecological mechanisms within networks, we found that both morphological matching and phenological overlap generally outperformed abundances in the explanation of interaction frequencies. Together, these findings provide insights into the ecological mechanisms that underlie geographical patterns in resource specialization. Notably, our results highlight morphological constraints on interactions as a potential explanation for increasing resource specialization towards lower latitudes.

Keywords: resource specialization, forbidden links, modularity, morphological matching, phenology, abundances, pollination.

Introduction

The mechanisms that underlie the structure of interaction networks is a frequently investigated topic in community ecology [1-3]. For mutualistic networks, these mechanisms often comprise morphologies, phenologies, and abundances, which all may influence the likelihood for species to interact [1, 2, 4-8]. Knowledge about which mechanisms determine interaction frequencies has implications for interpreting the drivers of resource specialization [9-12]. However, to date, only studies of single networks have addressed the relevance of morphologies, phenologies, and abundances for explaining interaction frequencies between mutualistic partners [6, 13-17]. Consequently, we still lack knowledge about how these ecological mechanisms may cause variability in resource specialization at large geographic scales.

Morphological matching is a frequently discussed determinant of mutualistic interactions [1, 5, 14, 17, 18]. In plant-pollinator communities, morphological matching often represents the similarity in length and shape between a flower's corolla and a pollinator's feeding apparatus [4, 19, 20]. Matching between these traits may lead to specialized network structures by limiting the species' access and preferences to a subset of mutualistic partners. Phenological overlap between interacting species is a mechanism that limits the available time for interactions to occur [2, 21]. Seasonal turnover in community composition may result in some mutualists having none or limited co-occurrence, and consequently, few possibilities to interact [2, 21, 22]. By constraining interaction probabilities, phenological mismatch is expected to increase a network's level of specialization. Lastly, the local variation in species abundances may influence the random chance for partners to interact [2, 3, 23, 24]. Specifically, under random encounters, the likelihood of interactions would be highest between abundant species [1, 5]. Interaction frequencies that reflect abundances would thereby predict a high overlap between the resource use of species, resulting in a low degree of network specialization [16, 18, 23].

The degree to which morphological matching, phenological overlap, and abundance explain interaction frequencies may depend on the environmental setting. The classical literature on diversity gradients suggests that the warm, humid and less seasonal climates of the tropics make natural selection more influenced by biotic interactions in comparison to temperate regions [25-28]. In turn, tropical climates could lead to a greater variety of morphological (co)adaptations and greater resource specialization [10, 25-28]. Accordingly, studies have found plant-hummingbird networks to become increasingly specialized towards the equator [10] and to coincide with greater diversity of hummingbird functional traits [8]. On this basis, one may hypothesize that the increase in resource specialization towards tropical regions coincides with an increased tendency of species to interact with morphological matching partners.

In contrast to morphological matching, to the best of our knowledge, there are no clear hypotheses on how phenological constraints on interactions vary across environmental gradients. Plant species in seasonal tropical regions usually have synchronized flowering periods during the rainy season, whereas phenologies are more staggered across the year in less seasonal regions [29]. If the phenologies of pollinator species follow the same pattern, mutualistic partners in seasonal environments should generally experience few phenological mismatches. In that case, we would expect phenologies to impose fewer constraints on interaction frequencies in seasonal environments than in less seasonal environments. If both morphological and phenological constraints on interactions are absent, we expect that species would interact randomly according to their relative abundances [18]. Thus, abundance should best explain interaction frequencies in cold, dry and seasonal environments [3, 24].

In this study, we use morphological matching, phenological overlap, and abundance to explain plant-hummingbird interaction frequencies at a large geographic scale. We focus our investigation on these three mechanisms, as they have previously been shown to influence

146 interaction frequencies within plant-pollinator networks [2, 5, 6, 14, 16]. First, we investigate how
147 the mechanisms may influence network-derived measures of resource specialization, and second,
148 how their explanation of interaction frequencies varies across environmental gradients (see ESM1
149 for a conceptual overview of our main hypotheses). To do so, we analyzed a unique dataset
150 consisting of 24 plant-hummingbird interaction networks distributed from Central Mexico to
151 Southern Brazil (20ºN-30ºS). For each plant and hummingbird species within these networks, we
152 have additional information on phenologies, morphologies, and abundances. We expected
153 morphological matching and phenological overlap to be more relevant for explaining interaction
154 frequencies in regions with low annual climate seasonality and high annual mean temperature and
155 precipitation [8, 10-12, 25, 26, 30]. It has been proposed that specialized co-adaptations increase in
156 tropical mountains due to the suitable preconditions for species to track changing climates [11, 31,
157 32]. Thus, we expected that morphological matching and phenological overlap would impose more
158 constraints on interaction frequencies in topographically complex areas in the tropics. Oppositely,
159 we expected abundance to have a decreased influence on interaction frequencies in specialized
160 networks sampled in areas with high topographical complexity, high mean annual temperature, high
161 mean annual precipitation, and low climate seasonality [16, 18].

162

163 **Methods**

164 *(a) Networks, abundance, phenology and species traits*

165 We compiled data on 24 quantitative interaction networks collected throughout the Americas, in
166 areas mostly or entirely covered with native vegetation [Table ESM2; updated dataset from 24].
167 The networks comprise 106 hummingbird species, 31% of all described hummingbird species in the

168 world according to the IOC World Bird List v.7.3 [33; ESM3], and 450 plant species belonging to
169 57 plant families (ESM4, see ESM5a for additional details on sampling).

170 The abundance of plant species was measured as the number of flowers produced per species
171 in each community throughout the entire sampling period. Flowers were counted in plots or
172 transects estimated regularly throughout the sampling period. The abundance of hummingbirds
173 within sites was measured in the field by counting the number of visual and aural detections of
174 individuals across transects (n=12 networks) or point counts (n=4 networks), or the number of
175 individuals captured by mist-netting (n=8 networks; ESM5a). Because the abundance sampling
176 protocols were not standardized among networks, we treated the data as relative abundance, i.e. for
177 all species we calculate their abundance as the proportion of the total number of individuals within a
178 given community. Still, we note that mist nets may be especially efficient for surveying elusive
179 understory species, such as traplining hummingbirds, whereas transects and point counts may be
180 better at surveying species at higher vegetation strata [34]. We recognize that the caveat inherent in
181 using different sampling schemes across networks may influence the outcome of our analyses.
182 However, as we used relative abundances to model interaction frequencies within networks (not
183 between networks), we believe that the different sampling schemes had a minimal influence on our
184 results.

185 The phenology of each plant and hummingbird species in each network was determined as the
186 presence-absence of, respectively, open flowers and individuals at each sampling period (usually
187 months). Flower morphology was characterized by the effective corolla length [sensu 35], measured
188 as the distance from the nectary to the corolla opening. The effective corolla length reflects the
189 minimum length of mouthparts required for pollinators to access the nectar legitimately.
190 Hummingbird bill morphology was measured as the length of the exposed culmen from captured
191 hummingbird individuals (see ESM5b further details on sampling).

192

193 *(b) Climate and topography data*

194 All climate variables were extracted as means within a 10 km radius around the location of each
195 network. Climate variables were downloaded from the WorldClim database in 30 arc second
196 resolution [36; v 2.0; http://www.worldclim.org]. We included mean annual temperature (MAT)
197 and precipitation (MAP), as well as seasonality in temperature (annual standard deviation in
198 monthly mean temperature; TS) and precipitation (annual coefficient of variation in monthly
199 precipitation; PS). Topographical data were retrieved from SRTM 90m DEM Version 4
200 (http://srtm.csi.cgiar.org). Within a 10 km zone around each network's location, we determined
201 topographical range as the difference between the maximum and minimum elevation.

202 *(c) Defining models for morphological matching, phenological overlap, and abundance*

203 We used the model for morphological matching presented in Sonne *et al.* [37], which assumes
204 pairwise interaction frequencies to decrease proportionally to the standardized difference in length
205 between the hummingbird's bill and the plant's floral corolla. In this framework, a hummingbird
206 with the longest bill has the highest probability of interacting with the longest flowers, while the
207 shortest-billed hummingbirds have the highest probability of interacting with the shortest flowers.
208 We calculated pairwise morphological matching for each hummingbird i and plant j within each
209 network k. We first standardized the hummingbird's bill length and the plant's corolla length to zero
210 mean and unit variance within networks and then calculated the Euclidean distance between each
211 pair of species ($\boldsymbol{M_{ijk}}$; see ESM6a for details).

212 In the phenological overlap model, pairwise interaction frequencies increase proportionally
213 to the number of sampling periods (usually months) in which hummingbird i and flowering plant
214 species j co-occurred in network k [$\boldsymbol{P_{ijk}}$; 2]. Random species encounters should generate pairwise

interaction frequencies that are proportional to the partners' relative abundances [2]. Therefore, the pairwise interaction probabilities in network *k* are calculated by multiplying the relative abundances of hummingbird *i* and plant *j* ($\boldsymbol{A_{ijk}}$). Prior to statistical modelling, $\boldsymbol{M_{ijk}}$, $\boldsymbol{P_{ijk}}$, and $\boldsymbol{A_{ijk}}$ were scaled to zero mean and unit variance.

(d) Linking ecological mechanisms with species' interaction frequencies

We used morphological matching (***M***), phenological overlap (***P***) and species abundances (***A***) to model interaction frequencies individually for each hummingbird and plant species. The modeling procedure was modified from Weinstein & Graham [38] as our data do not allow the estimation of interaction detectability. While the following model is described for hummingbirds, the same method was applied also to the plants.

The model assumes that the pairwise interaction frequency (Z) for each hummingbird species *i* in the network *k* follow a Poisson distribution with mean λ_{ik}, with the log link function of λ_{ik} predicted by the covariates: $\boldsymbol{M_{ijk}}$, $\boldsymbol{P_{ijk}}$, and $\boldsymbol{A_{ijk}}$. Model parameters were estimated using Markov chain Monte Carlo (MCMC). From there, we extracted posterior distributions of the standardized coefficients: β^{M}_{ik}, β^{A}_{ik}, and β^{P}_{ik}. As values of ***M*** are distances measuring morphological mismatch, a more negative β^{M}_{ik} value indicates greater ability of morphological matching to explain interaction frequencies. Conversely, more positive β^{A}_{ik} and β^{P}_{ik} values indicate better explanations of interaction frequencies by abundances and phenological overlap. These parameters were considered significant if less than 5% of their estimated posterior distribution overlapped with zero [38; see ESM6b for details on the model specification]. For each network, we determined the proportion of species with interaction frequencies significantly explained by morphological matching (*Imp.M*), phenological overlap (*Imp.P*) and abundance (*Imp.A*). We used these proportions as measures of each mechanisms' ability to explain the hummingbirds' interaction frequencies. We also calculated

239 the *relative* proportion of species by dividing *Imp.M, Imp.P,* and *Imp.A* by their within-network
240 sum. Thus, the relative proportions value represents the degree to which a given ecological
241 mechanism performs in explaining interaction frequencies relative to the remaining two
242 mechanisms. We present relative proportion values for each network as kernel density distributions
243 [39]. Here, the contribution of each network is weighted according to the richness of hummingbirds.

244 *(e) Linking ecological mechanisms with network structure*

245 We investigated whether morphological matching, phenological overlap, and abundances
246 influenced two measures of network structure that reflect resource specialization. First, we
247 calculated *complementary specialization* (H_2'), which quantifies the partitioning of interactions
248 relative to their availability [i.e. network marginal sums; 40]; it ranges between zero and one, with
249 higher values indicating higher partitioning of interactions between species in the community.
250 Second, we calculated *weighted modularity* (Q), which describes a network's tendency to comprise
251 subgroups of interacting species [9]. Modularity is high when species mostly interact with partners
252 from their respective modules. Modularity differs from specialization by quantifying the
253 partitioning of interactions between groups of species rather than between individual species.
254 Modularity was calculated using the DIRTLPA+ algorithm [41] using $10e^7$ steps. Due to the
255 stochastic nature of this optimization algorithm, we repeated the analysis 10 times for each network
256 and kept the highest Q value [9].

257 As empirical networks vary in species richness and sampling intensity, the observed values of
258 network structure, such as specialization and modularity may not be directly comparable [42]. To
259 overcome this issue, we used null models to calculate the extent to which the observed network
260 metric deviates from a null expectation. To compute the null model, we used Patefield's algorithm
261 [43], and then subtracted the observed values of network structure from the mean values obtained
262 from 1000 randomizations (Δ-transformation; See ESM7 for evaluation of alternative null models).

While we report the null model corrected values for modularity [40, 44], we report complementary specialization without the null model correction because this index is already subject to a correction for the marginal totals of the network. Nevertheless, we also ran analyses with the Δ-transformed version as reported in the supplementary material. All network analyses were conducted in R using the 'bipartite' package v. 2.11 [45].

We fitted linear models for complementary specialization and Δmodularity using the proportion of species within networks whose interaction frequencies were significantly explained by morphological matching (*Imp.M*), phenological overlap (*Imp.P*) and abundance (*Imp.A*). As additional explanatory variables, we included the network size, defined as the total richness of hummingbird and plant species, and a measure of sampling intensity, calculated as the square root number of interaction events divided by the total richness of hummingbird and plant species [46, 47]. We also tested for the potential confounding effect of spatial autocorrelation in the linear model residuals using the R package *ncf* [48]. To do this, we fitted Moran's *I* correlograms with 500 km distance classes and a truncation distance of 5000 km. Positive spatial autocorrelation was non-significant in all models, suggesting that spatial autocorrelation had no influence on our results (ESM8).

(f) Geographical patterns in ecological mechanisms' explanation of interaction frequencies

Separately for hummingbirds and plants, we fitted logistic models that regressed absolute latitude against *Imp.M, Imp.P, Imp.A*. To explore the effect of species richness and sampling, we ran supplementary models that included network size (total richness of hummingbird and plant species) and sampling intensity as explanatory variables (ESM9). We noticed that networks were not evenly sampled across the Americas, with the majority of networks occurring either in Central America/the Andes or along the Brazilian Atlantic coast (ESM9). To assess if the latitudinal trend was caused by

differences between these two biogeographical regions, we regressed absolute latitude against *Imp.M, Imp.P,* and *Imp.A* while including a dummy variable stating whether networks were located east or west of 60º longitude (i.e., occurred in Central America/Andes or along the Brazilian Atlantic coast).

Finally, we used logistic models to regress *Imp.M, Imp.P,* and *Imp.A* against network size and the following environmental variables: topographic range, mean annual temperature, mean annual precipitation, temperature seasonality, and precipitation seasonality. All possible model combinations were fitted and then evaluated using the Akaike Information Criterion with correction for small sample sizes (AIC_C). Usually, we found no single best model for the response variables, as ΔAIC_C was ≤ 2.0 between the model with the lowest AIC_C and several other models [49]. Therefore, we averaged the estimates from all possible model combinations weighted by Akaike weights (w_i). Additionally, we present the summed Akaike weights for all models containing each explanatory variable, Σw_i [49]. Model selection and model averaging were conducted using the 'MuMIn' package in R [50]. The goodness of fit for linear models was evaluated by McFadden's R^2 [51].

Results

The proportion of species interacting with morphologically matching partners (*Imp.M*) correlated positively with both metrics of resource specialization (*complementary specialization* and *modularity;* Figure 1). These correlations remained significant when accounting for the potential confounding influence of sampling intensity and network size (ESM10).

The tendency of species to interact with morphologically matching partners increased towards tropical latitudes (Figure 2). This trend remained after accounting for the clustering in network sampling between the Central America/Andes and Eastern Brazil, and when including network size

and sampling intensity as additional explanatory variables (ESM 9). For hummingbirds, we found phenological overlap to have a stronger influence on interaction frequencies towards tropical latitudes, while species' abundances better explained interaction frequencies towards higher latitudes, when including region (i.e. Central America/Andes vs. Eastern Brazil), network size and sampling intensity as explanatory variables (ESM9). For plants, however, phenological overlap better explained interaction frequencies within networks from Central America/Andes than within networks from Eastern Brazil (ESM9).

For both plants and hummingbirds, the explanation of interaction frequencies by morphological matching correlated negatively with temperature seasonality, which was the only predictor variable that remained present in all best-fitting models (ΔAICc < 2.0; Table 1). Phenological overlap best explained the hummingbirds' interaction frequencies in areas with low temperature seasonality (Table 1). For plants, phenological overlap best explained interaction frequencies in areas with high topographic range, mean annual temperature, temperature seasonality, and low species richness (Table 1). For hummingbirds, abundance best explained interaction frequencies in areas with high seasonality in precipitation and low seasonality in temperature (Table 1). Abundance was best explaining the plants' interaction frequencies in areas with high topographic range, mean annual temperature and temperature seasonality (Table 1).

Overall, we found that abundance generally had a weaker influence on interaction frequencies than morphological matching and phenological overlap (Figure 3).

Discussion

Across plant-hummingbird networks, we show that resource specialization increases with the tendency of species to interact with morphologically matching partners (Figure 1). Moreover, we found that morphological matching is a more prominent driver of species' interaction frequencies

when the networks are located closer to the equator (Figure 2). Together, these results highlight that the relevance of traits for explaining interaction frequencies is context dependent [7]. In some communities, traits matter more than in others, and this variability may contribute to the latitudinal pattern in resource specialization. In addition to morphologies, we found phenologies to be important for determining interaction frequencies, more so than the local variability in abundance (Figure 3). Based on our findings we speculate that partitioning of ecological niches, by morphological matching and phenological overlap, could be important for maintaining coexistence within diverse communities of interacting species.

The fact that morphological matching best explained interaction frequencies closer to the equator is consistent with the classical view of tropical environments as favorable to biotic specialization, either through co-evolutionary adaptations or ecological fitting [10, 25, 52, 53]. Still, the idea that biotic specialization increases towards the tropics has remained a subject of debate, as empirical studies have presented idiosyncratic results [10, 46, 47, 54, 55]. Previous work on our hummingbird-plant networks showed that network-derived resource specialization increases towards tropical latitudes [10], and coincides with high diversity of hummingbird traits [8]. Our study goes beyond previous macroecological analyses of network structure [8, 10, 11], and targets the potential ecological mechanisms that may constrain the likelihood for partners to interact. We recognize the caveat inherent to the geographical distribution of our sampling localities (Fig. 2), and that expanding the sampling to cover a wider latitudinal gradient would be important to strengthen our conclusions. Yet, the results presented here bring us closer to a mechanistic understanding of how morphological traits may influence the variability in resource specialization across environmental gradients.

Beyond the latitudinal patterns, we also found that morphological matching best explained interaction frequencies in areas with low temperature seasonality (Table 1). Annual temperature

stability is one of the most important characteristics of tropical climates [56]. The lower seasonality of tropical regions causes resources to be present throughout the year, which may lay a foundation for plants and pollinators to develop specialized associations [11, 25, 26, 57]. Moreover, theory suggests competition to be more influential on community structure in the absence of environmental filters, as within the tropics [27, 30, 57]. Thus, we speculate that interspecific competition within guilds together with diffuse mutualistic coadaptations may contribute to the high degree of resource specialization within the tropical regions [8, 15, 58, 59]. Similar to morphological matching, phenological overlap had a stronger influence on hummingbird's interactions in areas with low temperature seasonality (Table 1). This result concurs with our hypothesis that seasonal climates cause more synchronized flowering periods among plant species in comparison to aseasonal climates. When plants synchronize their flowering, each pollinator species may overall experience fewer phenological mismatches with their mutualistic partners. For the plants, however, the same association pointed in the opposite direction: phenological overlap had a stronger influence on interactions in areas with a high temperature seasonality (Table 1). This result may be driven by hummingbirds with migratory behavior, which are more common in seasonal regions. Hummingbird migrations could impose higher seasonal turnover in species composition, thereby causing higher phenological constraints to the plants' interactions. Regardless of the underlying explanation, the idiosyncratic results between hummingbirds and plants highlight that the environmental conditions that cause seasonal species turnover may depend on the ecological guild. Contrarily to morphological matching and phenological overlap, our results do not support the idea that abundance is a general explanation for why some interactions occur more frequently than others. Thus, although abundant hummingbirds may be more generalized in their floral preferences [24], our result suggests that abundant species do not necessarily have the most frequent interactions with abundant partners. Thus, although phenology and to a lesser extent abundance also

matter, we have identified morphological matching as a key determinant of species' interaction frequencies.

The most challenging aspect of documenting morphological matching in plant-hummingbird networks is the fact that hummingbirds can extend their tongue to access the flowers' nectar. As such, the absolute difference between bill length and flower depth is not an accurate representation of the actual morphological mismatch. Our model for morphological matching builds on the assumption that hummingbirds with the relatively longest bills should prefer flowers with the longest corollas. Thereby the model anticipates morphological matching to affect the hummingbirds' floral preferences without making specific assumptions about how much their tongues can be extended. The model also implies that long-billed hummingbirds should interact less with short flowers [13]. The ecological explanation for this may be twofold. First, long-billed hummingbirds could minimize competition with short-billed species by using preferentially the flowers with the longest corollas [20]. Second, flowers with short corollas typically have low nectar volume, which could make them unprofitable for long-billed hummingbird [20, 60]. Therefore, both interspecific competition between hummingbirds and variability in the flowers' nectar reward may also explain why morphological matching contributes to a high degree of resource specialization [35, 60].

When compared to other avian pollination systems, hummingbirds and plants have the most specialized morphologies and the highest level of resource specialization [20, 61, 62]. Moreover, pollination networks are usually more specialized than seed dispersal networks, which is another common form of plant-bird mutualism [63]. In plant–frugivorous bird communities, network-derived specialization has previously been shown to increase towards temperate latitudes [47], but dietary specialization, i.e. the proportion of obligate frugivores, increases towards tropical latitudes [46]. As such, one may obtain opposing results depending on the scale at which resource

specialization is measured. While only some fruit-eating birds are specialized frugivores, all hummingbirds rely mostly on nectar as a food resource. Hence, plant-hummingbird networks should be a suitable system to investigate morphological matching. Although, many orders of insect pollinators have specialized adaptations to nectar extraction, they are also found collecting other floral resources [64]. In bees, for instance, tongue-lengths may affect floral preferences during nectar-gathering, but flowers with inaccessible nectar may still receive visits when bees are collecting pollen [64]. Plants and hawkmoths exhibit some highly specialized coadaptations, and this is probably the closest analog to a system in which morphological matching is crucial for determining interaction frequencies [65].

The mechanisms underlying the structure and organization of ecological communities have remained poorly understood at the large geographical scale. Using plant-hummingbird networks distributed across the Americas, we have identified morphological matching as a potential key driver of geographical patterns in resource specialization. Notably, closer to the equator, species tended to show stronger preferences for mutualistic partners with morphologically matching traits. Thus, our findings support the hypothesis that trait-mediated resource specialization increases towards lower latitudes.

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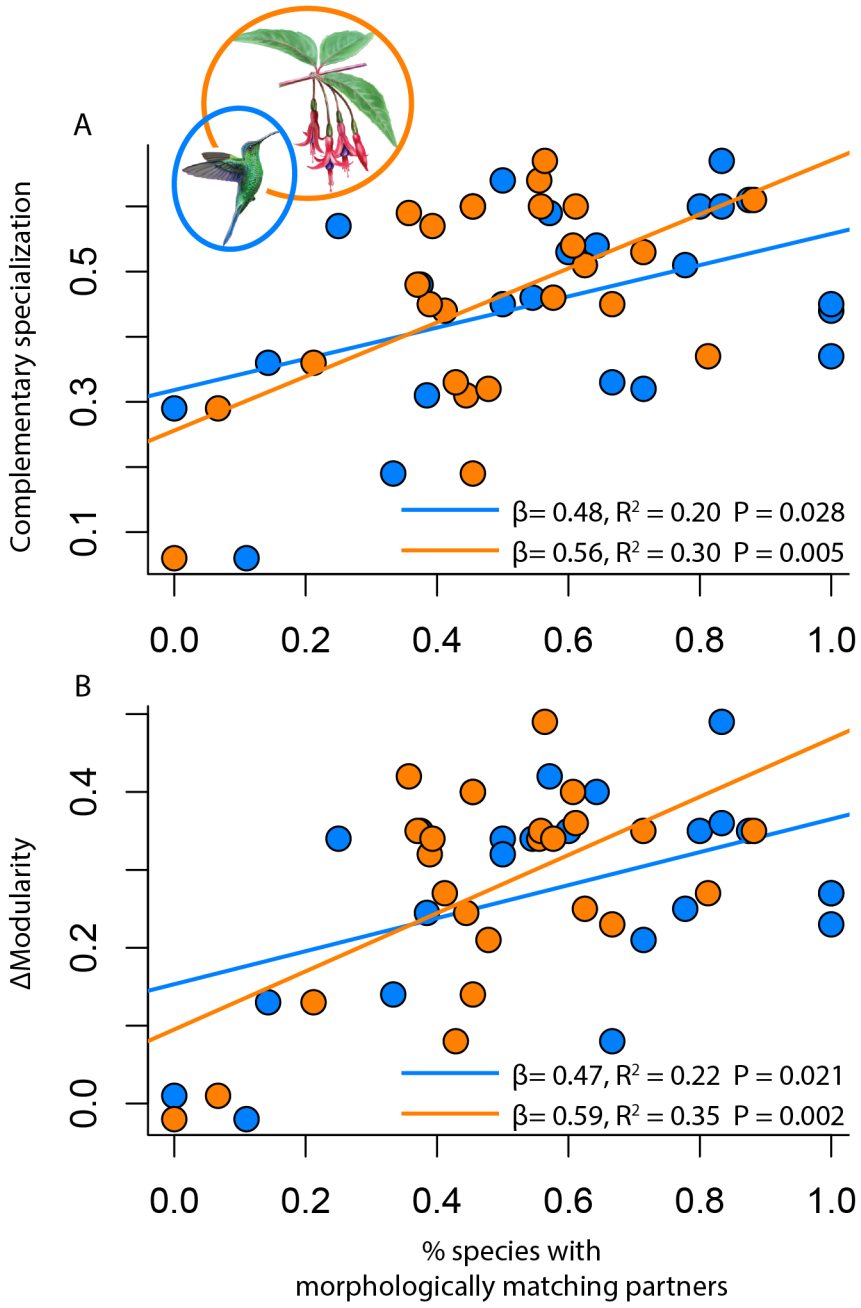
Tables

Table 1. Model selection and averaging results of logistic models fitted on different ecological mechanisms' ability to explain interaction frequencies within networks (n =24). The analyses were repeated individually for hummingbirds and plants. The response variables comprised the proportion of species within networks whose interaction frequencies were significantly explained by morphological matching (*Imp.M*), phenological overlap (*Imp.P*), and abundance (*Imp.A*). Explanatory variables include *Network size*: total richness of hummingbirds and plants within networks; *Topographic range*: maximum elevation subtracted from minimum elevation*; Mean annual temperature*; *Mean annual precipitation*; *Temperature seasonality*; and *Precipitation seasonality*. Goodness of fit is assessed by McFadden's R^2. Σw_i: Sum of 'Akaike weights' from all models including the predictor variable. MAM: standardized coefficients of variables present in all minimum adequate models (ΔAICc < 2). N_{MAM}: number of minimum adequate models. AVM: standardized coefficients of the averaged model across all models including a focal predictor variable.

Figures

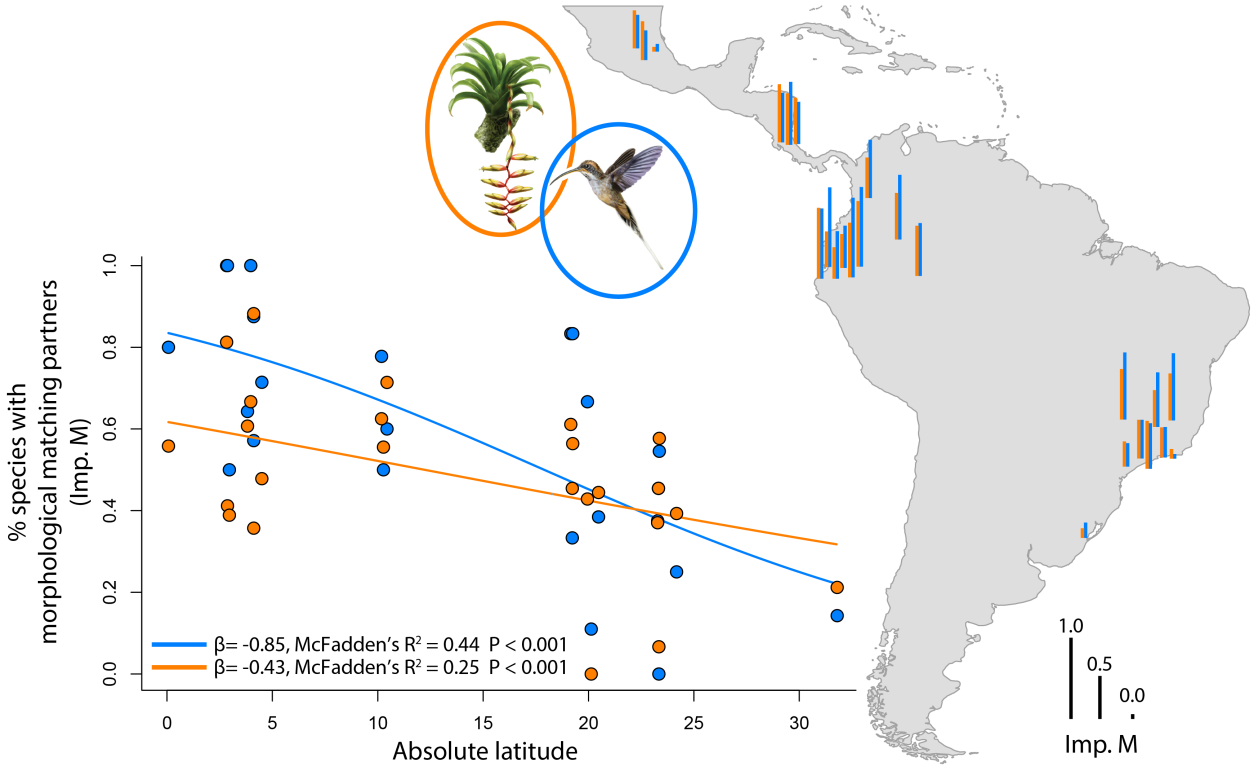
Figure 1. Linear models depicting the relationship between resource specialization and species' morphological matching. Resource specialization was measured as complementary specialization (A), and Δmodularity (B). Δ indicates a correction by the *Patefield* null model (see Methods). The x-axis shows the proportion of species within networks that exhibited a significant tendency to interact with morphologically matching partners. The linear models were run separately for hummingbirds (blue) and plants (orange). Drawings by Pedro Lorenzo.



457

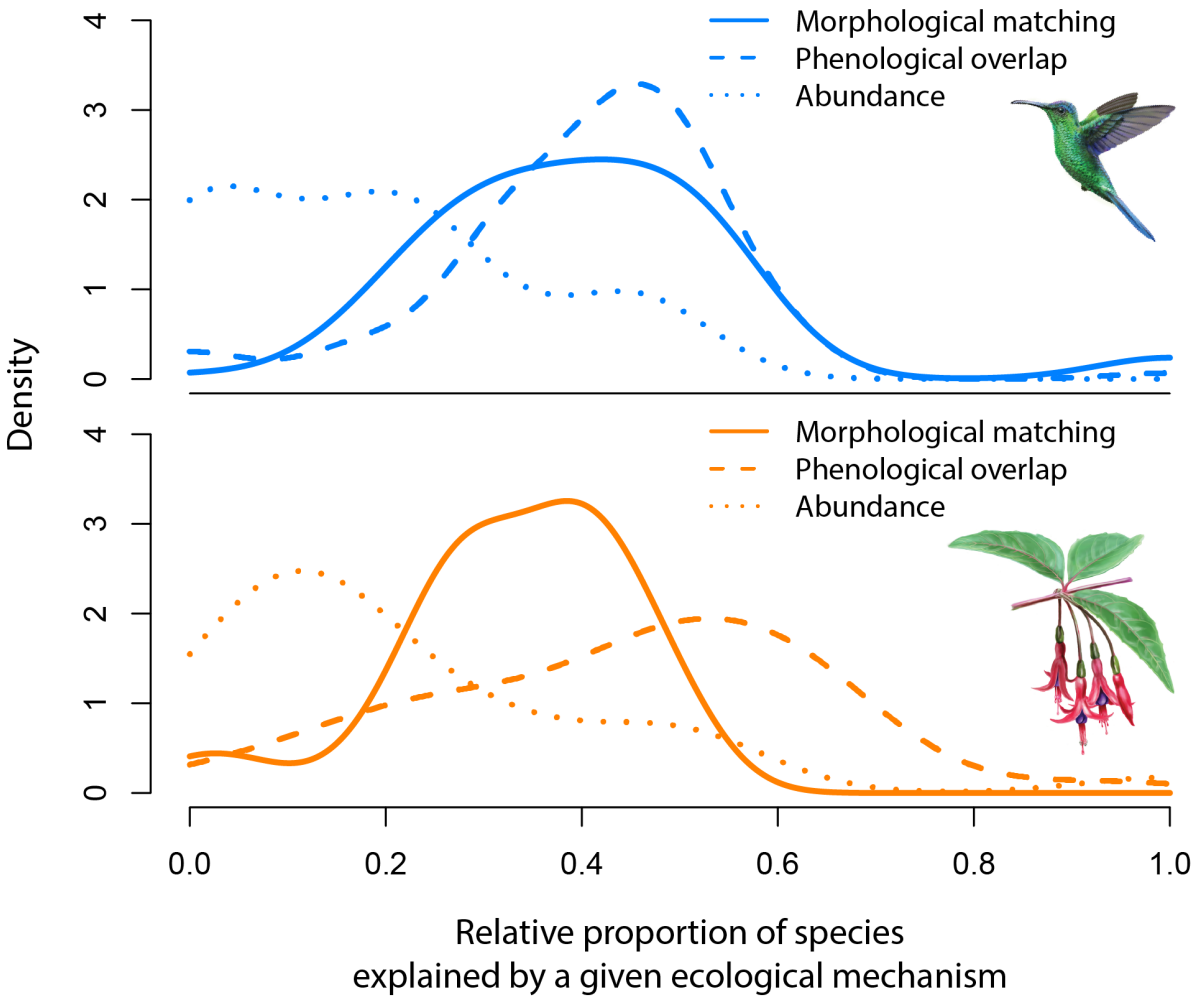
458 **Figure 2.** Geographical distribution of the 24 plant-hummingbird networks. The height of the bars
459 reflects the proportion of hummingbird species (blue) and plant species (orange) within networks
460 that showed significant tendencies to interact with morphologically matching partners (*Imp. M*).
461 Some points on the map have been slightly separated to improve visual clarity. The scatterplot

462 shows the negative relationship between *Imp. M* and absolute latitude, modeled by logistic
463 regression. Drawings by Pedro Lorenzo.



464

465 **Figure 3**. Kernel density distributions depicting the relative contribution of morphological
466 matching, phenological overlap, and abundance to the explanation of species' interaction
467 frequencies. The x-axis shows the proportion of hummingbirds (blue) and plants (orange) within
468 networks whose interaction frequencies are significantly explained by morphological matching,
469 phenological overlap and abundance, respectively. Each of these values was divided by their
470 within-network sum, thereby obtaining a *relative* proportion of species. Relative proportion values
471 higher than 0.50 indicate that a particular ecological mechanism was more effective at explaining
472 interaction frequencies than the two remaining mechanisms combined within a given network.
473 Drawings by Pedro Lorenzo.


Density
0
1
2
3
4
Morphological matching
Phenological overlap
Abundance
Morphological matching
Phenological overlap
Abundance
0.0
0.2
0.4
0.6
0.8
1.0
Relative proportion of species
explained by a given ecological mechanism

474

475

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